TABLE 2. Bluehead wrasse preferences for different body parts of host fishes. (+) average number of nips is greater than expected; (-) average number of nips is less than expected; (0) average number of nips does not deviate from expected based on G-test results.

Host species	head	gills	mouth	main body	pectoral fin	dorsal fin	ventral fin	tail fin
princess PF	0	0	-	0	0	+	+	-
yellowtail dml	0	0	0	-	+	0	0	-
redband PF	0	0	0	+	+	0	+	-
striped PF	0	0	0	+	0	0	0	-
blue chromis	+	0	+	-	-	-	-	+
stoplight PF	0	0	0	+	0	0	0	0
ocean surgeon	0	0	0	0	0	0	0	0

A COMPARISON OF FISH COMMUNITIES ASSOCIATED WITH ISOLATED *MONTASTREA* AND ELKHORN CORAL HEADS

CARTER D. WRAY AND IAN J. STEWART

Abstract. Many studies have shown different fish communities to be associated with different broad habitat types in a coral reef environment (Bell and Galzin 1984, Kaufman and Ebersole 1984, Sale 1977). We attempted to study niche separation on a small scale, through a survey of isolated coral heads. The coral species *Montastrea annularis* and *Acropora palmata* (elkhorn) represent different physical structures and are the main source of vertical relief on the fore reef at Discovery Bay. We hypothesized that similarly sized *Montastrea* and elkhorn coral heads in similar depths would support different fish assemblages. We also predicted that these assemblages would not change over the short time span of our study. We found this to be true, observing a total of 25 species on *Montastrea* heads and 18 species on elkhorn colonies, with only 14 species common to both. Species similarity indices were higher when both elkhorn corals and *Montastrea* heads were compared to themselves over time, than was the similarity between the two. These results could indicate some niche separation in these fish species and seem to support a habitat preference theory based on physical characteristics. Changes in reef-wide communities as the coral colonies recover from hurricane damage may also alter species abundances or niche selection by these species as relative proportions of the two coral types change.

INTRODUCTION (IJS)

Populations of fish on coral reefs represent an extremely diverse community. Many studies have shown that there are differences in these communities over broad habitat types such as back reefs, fore reefs or lagoons. Few species utilize all regions of the reef environment (Sale 1977). Even portions of the same fore reef separated by only 100 m can support distinct fish assemblages (Kaufman and Ebersole 1984). Bell and Galzin (1984) demonstrated that percent live coral cover can be one of the factors that significantly influences the number of individuals and species found on a reef. Because changes of only a few percent were associated with different assemblages it appears that fish community structure is directly related to coral species abundance.

On a smaller scale, Clarke (1988) found that on patch reefs, the size of the patch was closely related to the number of species present. Bizzarro et al. (1992) studied the relationship between rugosity, vertical relief and number of fish species present in small plots. They found that absolute vertical relief was directly correlated with rugosity, and that as both of these increased the number of associated species increased correspondingly.

Because coral reef fish have relatively small home ranges (Sale 1977), their habitational and nutritional needs could lead to some niche differentiation through habitat selection. Both recruitment location and subsequent differential mortality may act to cause some reef fish to be commonly found only in certain habitat areas. Lirman (1994) found evidence of this in that *Stegastes planifrons* (three-spot damselfish) select dead and live coral habitats for juvenile and adult territories, respectively. Other fish-habitat interactions such as gobies with sponges, brain corals and some fish species with anemones provide further examples of niche differentiation in the form of specific habitat needs.

At Discovery Bay, the percent coral cover on the shallow sections of the fore reef was substantially reduced during hurricane Allen in 1980. Dense stands of *Acropora*

palmata (elkhorn coral) were destroyed and what remained was predominately corals with compact growth forms such as *Montastrea annularis* (Woodley et al. 1981). These mound-shaped coral structures now represent a large part of the vertical relief in the fore reef habitat. The remainder consists of isolated living elkhorn colonies and dead colonies of both species in various stages of decay. These 'islands', in areas of mostly broken coral rubble , appear to act as a significant part of the home ranges of many fish species.

We hypothesized that similarly sized *Montastrea* and elkhorn coral heads ,in similar depths of water, would support different fish species assemblages. Fish species with small home ranges and specific habitat needs should be more suited to one species of coral and the physical structure it provides than with the other. We further predicted that there may be differences in assemblages within one coral species for live and dead colonies, as food resources and small habitat changes associated with the decay of the corals and algal growth may provide different microhabitats. We further hypothesized that over the short time period of our study these assemblages would not show significant changes.

METHODS (IJS)

We conducted our survey on the fore reef at Discovery Bay, Jamaica, West Indies. All data was collected while snorkeling in depths of 3-6 m.

On 3-4 February 1995, we located 40 isolated (>2 m to nearest structure) coral heads near the Canoe Cut on the west fore reef. We selected 10 of each of the following types of coral heads: those dominated by living *Montastrea*, those consisting of dead *Montastrea*, those dominated by living elkhorn colonies and those of dead elkhorn coral. For each, we measured height (total vertical relief off the substrate), width and length, then marked the coral head for later location. The volume of each coral head was then calculated. We attempted to control for size variation between coral heads and accepted only those coral colonies that had volumes between 0.3 m^2 and 0.85 m^2.

On 5-6 February we surveyed each of the 40 coral heads, between 0900-1130 or 1400-1630. Each survey was designed to give a comprehensive population for each fish species present. We first spent 5-10 minutes hovering over each coral head, recording all individuals within 0.5 m of the head, that were not deemed to be part of a transient school. Fish that left the immediate area of the coral head during the survey were not counted. The next 5-10 minutes was spent peering into crevices, under the head and between protrusions of coral to locate the smaller and more cryptic species. We continued this search until satisfied that we had eliminated potential bias toward omission of cryptic species (Brock 1982) and recorded all fish present. Urchins, crabs, shrimp, and starfish were also recorded.

On the 6-7 February we re-surveyed the first 20 coral heads located (5 of each type). The same procedure was used, although due to rough seas and poor visibility there may have been some variation in sampling effectiveness.

Coral Descriptions

Montastrea is one of the most common corals in the Caribbean (Kaplan 1982). The coral heads we sampled were generally of cylindrical shape, with living coral tissue covering the top of the mound. Crevices and holes were common on the top of the mound between and around coral polyps. Light algal cover was occasionally present on the sides of these corals and there were generally larger crevices (ca. 10-40 cm deep) beneath the mound.

Elkhorn corals are generally found near the reef crest and have flattened branching colonies resembling American moose antlers (Kaplan 1982). These branches were generally attached to a central point, which created an open shaded region below the branches. There were commonly some dead branches below the live ones in various stages of decay. Because of this there was an area of crevices and holes that was more open than *Montastrea* but more enclosed than the above branches. This structure provided a larger shaded area, but far fewer small holes and crevices than did *Montastrea*.

Statistical Analysis

Species similarity indices were calculated following the methods of Sale and Dybdahl (1978). Euclidean distance was used as a measure of similarity between fish communities, where:

$$D_{ij} = [\Sigma(k=1\text{-}s)\ (P_{ik}-P_{jk})^2]^{.5}$$

D_{ij} is equal to the distance between samples *I* and *j* , where s is the total number of species considered , P_{ik} is the proportion of fish in sample *i* that are of the kth species and P_{jk} is the equivalent proportion of fish in sample *j*. A high Euclidean distance correlates to a low similarity between the two compared communities.

Statistical comparison of distances was performed by random pairing of *Montastrea* and elkhorn coral heads, and by pairing *Montastrea* as well as elkhorn heads to the re-surveys 3-4 days later.

We attempted to control for size variation between samples, but were still faced with a natural range in volumes. With adequate analysis, incorporating this size variation in a three-way ANOVA comparison, this potential confounding factor could have been accounted for. However we did not have sufficient analytical means for testing in this manner. Size differences were not found to be significantly different when compared independently of other factors and so were not taken into consideration in future tests.

RESULTS (CDW)

The volumes of the four types of coral heads overlapped broadly (Fig. 1) and did not differ significantly (Table 1). Heads of live *Montastrea* had higher total species richness per head than the other three types (P= 0.018, Fig. 2, Table 1) although there was no difference in richness of solitary species (Table 1). This difference in species richness appears to result from more schooling species associating with *Montastrea* heads. There was also no difference in the number of individuals associated with each type of head, either for all species or just solitary ones (Table 1).

We observed a total of 29 species, 14 of which were associated with both *Montastrea* and elkhorn heads (live and dead combined), four of which were only associated with elkhorn, and 11 of which were only associated with *Montastrea*. Of the 25 species associated with *Montastrea*, four occurred only on live mounds, and five

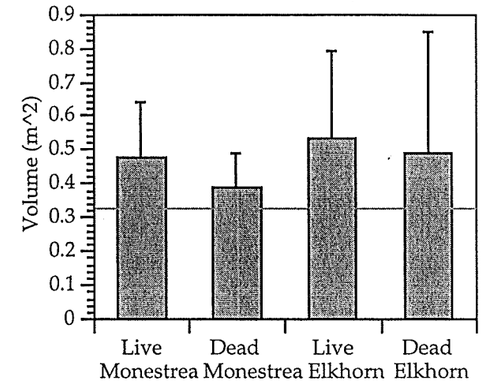

Fig. 1 volume of coral heads: means + upper ranges. the lower range for all four coral types ≈0.32 m^2 (gray line, N=10 for each)

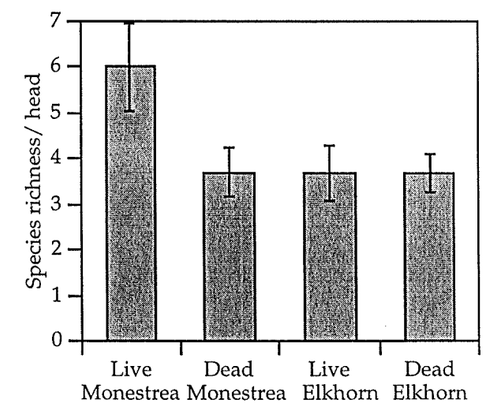

Fig. 2 species richness of coral heads by type: means ± SE (N=10 for each)

only on dead ones, although all nine of these species were only found on one head. Of the 18 species associated with elkhorn corals, five were only associated with dead heads, and two were only associated with live heads. Of these seven species, six only occurred on only one head, and the other was trumpetfish. Two trumpetfish were associated with live elkhorn heads, although individuals were observed associating with dead elkhorn heads that we did not sample. A list of all species sighted at each head is included in Appendix A.

The species or groups that were more commonly associated with *Montastrea* than elkhorn mounds (both living and dead) included groupers (family Serranidae, includes coney, grasby, and harlequin bass, U= 261.500, df= 1, P= 0.017), red spotted hawkfish (U=260.500, df= 1, P=0.019), sharpnosed puffer (U= 60.000, df= 1, P= 0.009), and sea urchins (class Echinoidea, includes long-spined and slate pencil urchins, U=91.000, df= 1, P= 0.008, Fig. 3). Other species only occurred near one species of coral but were too rare for the differences in their abundance to be significant. For elkhorn this included the longjaw squirrelfish, glassy sweeper, trumpetfish, and Spanish hogfish, while for *Montastrea* this included the greater soapfish, plain squirrelfish, reef squirrelfish, cardinal soldierfish, barred cardinalfish, roughhead blenny, blue chromis, brown chromis, and some invertebrates.

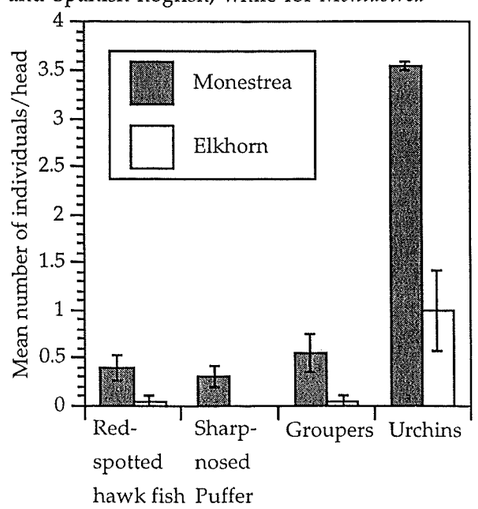

Fig. 3 Species more commonly associated with *Montastrea* heads than with elkhorn (N=20 for each).

The difference in species composition between randomly paired elkhorn and *Montastrea* heads, as measured by the Euclidean distance between the two (0.711 ± 0.0558, mean ± 1 SE) was significantly greater than between *Montastrea* mounds over four days (0.4862 ± 0.1223, P=0.0337) and between elkhorn heads over the same time period (0.2505 ± 0.0194, P=0.0001, Fig. 4, Table 1). The difference in species similarity between *Montastrea* mounds over time was also greater than that between elkhorn heads, although the difference was not significant (P=0.0525, Table 1). This may have been an artifact of the higher number of species associated with *Montastrea* than with elkhorn.

All species of fish found on each type of coral head during the re-sampling had already been found on the same type, with the following exceptions: two unidentified blenny species, one found on a live *Montastrea* mound and the other on a dead *Montastrea* mound, one bicolor damselfish found on a dead *Montastrea* mound, and a school of 18 bluehead wrasse on a dead *Montastrea* mound.

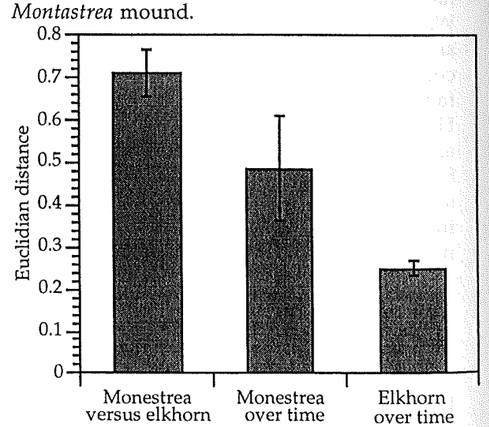

Fig. 4 Similarities between randomly paired *Montastrea* and elkhorn coral heads (N=20 pairs), between *Montastrea* heads initially and four days later (N=10 pairs), and between Elkhorn heads over the same time period (N=10 pairs).

DISCUSSION (CDW)

Although our study is limited by the short time-period over which it was done, our results support our hypothesis that different types of isolated coral heads support different fish communities, and that these communities show some degree of temporal stability. This indicates that fish species use different habitats selectively, and that niche partitioning is occurring on some level, which supports Clarke's statement that fish respond to subtle differences in patches and inhabit them selectively (1988). Sale's observation (1980) that "assemblages of reef fish are not particularly persistent in structure" may still hold true although the assemblages on a given head may change within a set of species that is specific for that coral type.

TABLE 1. Results of ANOVA tests.

	F	df	P
Number of solitary individuals per head	1.172	3,36	0.334
Number of solitary species per head	2.113	3,36	0.155
Total number of individuals per head	1.095	3,36	0.364
Total number of species per head	3.086	3,36	0.039
Euclidean distances	10.485	2,36	0.0002

The greater number of species associated with both live and dead *Montastrea* mounds than live and dead elkhorn heads indicates that more species sampled prefer the structure of *Montastrea* than elkhorn. This may be due to *Montastrea* having greater utilizable topographical complexity than elkhorn, although further study is needed to determine what types of topographical variation is usable by different fishes. Combined with an accurate quantification of the micro-topography of various coral species, this data could shed more light on niche partitioning and subsequent maintenance of diversity on coral reefs. It is also possible that competition for space on elkhorn is more intense, and limits the number of species that are able to associate with it.

The greater species richness per head of live rather than dead *Montastrea* mounds indicates that some aspect of living coral heads may allow them to support more species. This could be due to a loss of topographical complexity as dead mounds decay, which could result in a decrease in the number of species per head (Luckhurst and Luckhurst 1987). Live corals also have more zooplankton associated with them than dead coral (J. Gilbert, pers. comm.) which may increase the number of species that a coral head can support. It is not clear why this relationship does not hold true for elkhorn corals, although it may be that crumbled decaying elkhorn heads were not included in our sample, while dead *Montastrea* mounds of a similar age were surveyed.

That the number of individuals per head did not differ between live and dead coral colonies indicates that the positive correlation between percent live coral cover and fish densities (Bell and Galzin 1984) does not act on the level of individual heads. Areas with higher percent live coral cover may be able to support more "floater" fish that have larger home ranges than individual mounds, such as the hamlets, which were not included in our study. If this is so, such species may be more abundant in areas with higher percent live coral cover.

That different fish species associate with coral species that typify different successional stages supports Connel's intermediate disturbance hypothesis. A disturbance fish species that associates with the abundant enduring mound corals should have more available niches than those species associated with the more delicate branching corals, and should therefore be more abundant following a major disturbance. Conversely, as a reef nears successional climax, the species associated with the then dominant branching corals should be more abundant for the same reasons. In both cases, species associated with the less abundant coral type might be able to shift their realized niche from those that we observed. Overall diversity of coral reef fish may be highest at some intermediate abundance of mound and branching corals. At discovery

Bay, the species associated with *A. palmata* may become more abundant in the future, if the populations of that coral are able to recover.

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Appendix A: Volumes of coral heads (in m^2)

	1	2	3	4	5	6	7	8	9	10
Live Montastrea	0.32	0.37	0.54	0.5	0.64	0.50	0.60	0.50	0.38	0.43
Dead Montastrea	0.49	0.49	0.35	0.34	0.45	0.32	0.38	0.35	0.36	0.36
Live Elkhorn	0.64	0.70	0.68	0.79	0.42	0.60	0.42	0.42	0.36	0.33
Dead Elkhorn	0.60	0.49	0.49	0.85	0.54	0.33	0.40	0.40	0.46	0.36

Appendix B: continued

Coral type	Live Montastrea										Dead Montastrea										Live Elkhorn										Dead Elkhorn									
Number	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Bodianus rufus (spanish hogfish)																						1																		
Canthigaster rostrata (sharpnose puffer)			[1]			1						1	1																											
Gobiidae fam. sp. (unidentified)	[1]	[1]	1	1	2		1																																	
# of non-schooling spp.	4	4	4	3	9	8	2	8	3	4	5	5	4	6	1	1	2	6	4	4	2	5	7	2	3	4	3	3	3	2	5	4	4	2	5	1	3	4	4	2
# of non-schooling ind.	4	5	4	11	10	3	8	5	5	7	7	6	6	1	1	2	6	5	5	4	6	11	3	5	7	7	3	2	3	5	2	5	8	5	3	5	2	4	5	3
Schooling fishes:																																								
Chromis cyanea (blue chromis)											1																													
C. multilineata (brown chromis)				[7]																																				
Thalassoma bifasciatum (bluehead wrasse)				10							1																													
Total # of spp.					[9]	8	2	8	3	4	5	5	4	6	1	1	2	6	4	4	2	5	7	2	3	4	3	3	3	2	5	4	4	2	5	1	3	4	4	2
Total # of ind.				[10]	12	3	8	5	5	7	7	6	6	1	1	2	6	5	5	4	6	11	3	5	7	7	3	3	3	3	5	4	4	2	5	2	3	4	3	3
Invertabrates:																																								
Diadema antillarum (long-spined urchin)		4	5	8	27	19	22	3	16	11	8	24	7	6	6	1	18	2	6	5	5	4	38	27	3	5	7	7	3	2	3	3	21	6	29	22	2	2	4	8	5	33	4
Eucidaris tribuloides (slate-pencil urchin)		4	4	4	11	9	2	9	4	5	8	5	4	6	1	3	2	6	4	4	2	6	8	2	3	4	3	3	3	2	3	4	5	3	6	1	3	4	4	4	3	4
Amphinomidae fam. sp. (fireworms)				1																																				
Ophiurae order sp. (brittlestars)							1																																	
Brachyura section sp. (true crabs)					[1]																																			
Natania suborder sp. (shrimp)					2																																			
Fasciolaria tulipa (true tulip snail)																																								

Appendix B: Fish associated with live and dead *Montastrea* and elkhorn coral heads.

Coral type	Live Montastrea										Dead Montastrea										Live Elkhorn										Dead Elkhorn									
Numer	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
Microspathodon chrysurus		1			2		1	1		1	1						1				2	1	2	2	2	3	1	1		1	1	1	3	1		1	1			1
(yellowtail damselfish)		[1]	[1]		[1]						[2]		[1]								[2]	[1]	[3]	[1]	[1]							[1]	[3]	[1]	[1]					
Stegastes fuscus		2		2			1				2	1	1	1			3		1		1	3		2	3	3	1	1	2	1	3	2	1		2	2				
(dusky damselfish)		[2]									[1]		[1]	[2]	[1]						[1]	[3]	[1]	[2]	[3]						[2]	[2]	[1]		[2]					
S. partitus				1	1		1	2																							1	1		1						
(bicolor damselfish)				[2]	[1]							[1]																			[1]			[1]						
S. variabilis	1	1	1	1	1	2	1		1	2		3	1					1	2	3							1					1					1	1		
(cocoa damselfish)	[1]		[1]	[1]	[2]								[1]																			[1]								
S. planifrons	1						1	2	2	1						1		1				1														1	2	2		
(threespot damselfish)	[1]		[1]		[1]						[2]	[2]																												
Holocentrus adscensionis											1																													
(squirrelfish)											[1]																													
Neoniphon marianus																																		1						
(longjaw squirrelfish)																																								
Surgocentron coruscus							1																																	
(reef squirrelfish)																																								
Myripristis jacobus											2											3																	2	
(blackbar soldierfish)											[2]											[3]																		
Plectrypops retrospinus																	1																							
(cardinal soldierfish)																																								
Apogon binotatus					1																																			
(barred cardinalfish)																																								
Pempheris schomburgki																					1																			
(glassy sweeper)																					[1]																			
Fistularia tabacaria																						1	1																	
(trumpetfish)																							[1]																	
Cephalopholis fulvus				1	1								1																											
(coney)																																								
C. cruentata				1																																				
(grasby)																																								
Serranus tigrinus				1			1			2	1		1		1																	1								
(harlequin bass)				[1]																																				
Rypticus saponaceus					1																																			
(greater soapfish)																																								
Amblycirrhitus pinos	1			1	2											1		1	1	1																		1		
(redspotted hawkfish)	[1]		[1]		[1]								[1]																											
Blenniidae or Clinidae																		1																	1	1				
fam. sp. (unidentified)					[1]								[1]																		[1]	[1]								
Ophioblennius atlanticus			2						1								1	1			1	1		1	1	1			1	1				2						1
(redlip blenny)			[1]																		[1]		[1]										[1]	[2]						
Malacoctenus triangulatus	1				1								1												1													1		1
(saddled blenny)	[1]		[1]										[1]																											
Acanthemblemaria spinosa												1																									4		
(spinyhead blenny)												[1]										[1]																		
A. aspera												1																												
(roughhead blenny)																																								